SHORT COMMUNICATION

NOTES ON THE NATURAL HISTORY AND HUNTING BEHAVIOR OF AN ANT EATING ZODARIID SPIDER (ARACHNIDA, ARANEAE) IN COLORADO

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ABSTRACT. The ant hunting behavior of *Zodarion rubidum* (Araneae, Zodariidae) is described from specimens collected in Colorado, USA. Like other members of this genus, *Z. rubidum* constructs iglooshaped stone retreats under rocks and feeds on ants. Details of the prey capture behavior are provided including initial and subsequent reactions of ants to the bites of *Z. rubidum* and data on the time it takes for ants to become completely paralyzed as a result of the bites.

Keywords: Zodarion, myrmecophagy, spider-ant association, femoral organ

Zodarion rubidum Simon 1914 is the only species of this genus of Zodariidae reported from North America (Vogel 1968; Jocqué 1991; Bosmans 1994, 1997). It had previously been reported from Pennsylvania (Vogel 1968; Bosmans 1994, 1997). Participants of the Colorado Spider Survey, Nina Shilodon and Steven Bonham, discovered the first population of this small spider in Colorado. The Colorado population lives under rocks inside igloo-shaped stone retreats in a variety of habitats including xeric and riparian areas. Most members of the genus build these retreats (Simon 1914; Harkness 1977; Jocqué 1991; Bosmans 1994; Pekár & Král 2001). The spider forms the retreat by overlapping small pieces of debris (soil particles, rocks, and plant material) on a silken framework using its palps and front legs to manipulate material (see figure 3 in Pekár & Král 2001). Although Vogel (1968) did not find these retreats in a population of Z. rubidum found in a rock quarry in Pennsylvania, it is likely that they are present in that population as well. It is unknown whether this species extends across the US between Pennsylvania and Colorado. Although it has not previously been reported from collections from those areas, collectors not specifically searching for them may easily overlook the small retreats.

Spiders in the genus *Zodarion* are compulsory ant eaters, or myrmecophages (Simon 1874, 1914; Santschi 1908; Schneider 1971; Harkness 1976, 1977; Jocqué 1986, 1991; Couvreur 1990a). The purpose of our study was to examine the ant hunting, or myrmecophagic, behavior of these spiders in more detail in a controlled laboratory setting.

Thirty immature spiders were collected in July 1999 from a riparian area off W. 56th Avenue west of the town of Golden, Colorado in Jefferson County (39°48' N, 105°14' W; 1,859 m). Spiderlings were individually housed in Petri dishes measuring 55 or 90 mm in diameter. Loose soil and wet cotton were provided for each spider. A fluorescent light was placed on a timer providing a 12:12 light:dark cycle. This proved to be an important element of our protocol because these spiders appear to be strictly nocturnal; within 24 h all 30 immature spiders had constructed retreats and remained hidden during the light period, venturing out only during the dark period to forage/hunt. Pekár & Král (2001) recorded activity peaks for this species early in the morning from 0600-0900 h and in the evening from 1830-2200 h but did not monitor the nocturnal activity of this species. Couvreur (1990b) provides data indicating that this species is active at night. Entrance openings were visible on the retreats of some spiders while others plugged the entrance with rocks or soil particles. Of the 30 spiderlings, 16 were used for feeding experiments. Voucher specimens have been deposited in the arachnid collection at the Denver Museum of Nature & Science.

Three-four hours after the onset of the dark period the dishes were checked for spiders that had emerged from their retreats using a light with a red filter. In order to conduct feeding experiments, ants were gathered from another collecting site where *Z. rubidum* was also found off Easley Road on North Table Mesa in Golden, Colorado, Jefferson County

(39°46'31" N, 105°11'30" W, 1,762 m). These ants were identified as *Lasius niger* var. *americanus* (Emery 1893) (Formicinae) and *Myrmica* sp. (Myrmicinae). These ants are active both during the day and at night in the field (personal observation). We conducted 26 feeding trials among these 16 individuals. Although seven spiders were observed more than once, each of the 26 feeding trials was treated as an independent event since at least one week elapsed between trials.

For each trail, a single ant was placed into each of the dishes with an active spider and the behaviors of the spider and the ant were observed using a stopwatch to time events. These interactions were observed through an Olympus SZH stereo-microscope with a red acetate filter placed over the light source or over the Petri dish to minimize the influence the light may have had on the spiders' behavior.

The 16 spiderlings used in the feeding trials were divided into three arbitrary Size Classes: Size Class A included three juveniles 1.7-1.9 mm in length; Size Class B included nine spiderlings 2.0-2.2 mm in length; and Size Class C included four spiderlings 2.3-2.6 mm in length. In comparison, adult spiders ranged in size from 2.09-2.87 mm (n = 8; including four males and four females). We recorded the following data: 1) the time between the initial bite and reaction of the ant (immediate response, response 1-20 sec after bite, response 21-40 sec after bite); 2) the location of the initial bite (rear leg of ant, middle leg, front leg, antenna, abdomen, unknown); 3) the initial reaction of the ant to the bite; 4) subsequent reactions of the ant; 5) whether the spider bit more than once; and 6) the time from the initial bite to complete paralysis.

Prior to the encounters with the spiders, ants moved randomly around the Petri dish, antennating the substrate and sometimes picking up sand or other material with their mandibles. In 18/26 trials, the ant reacted immediately to the spider's bite, stopping its random movements and showing a distinct response; in 5/26 trials the ant reacted 1-20 sec after being bitten; in 3/26 trials initial reaction was 21-40 sec. In four of the trials, the attack by the spider was so rapid that it was not possible to determine with certainty where on the ant's body the initial bite was delivered. In the 22 attacks that could be scored, the ants were initially bitten more often on their rear legs (11/26 times) than on the middle legs (4/26 times), the front legs (5/26 times), the antennae (1/26 instances), or the abdomen (1/ 26 instances). Statistical analysis showed that the rear legs were bitten significantly more often than expected and the antennae were bitten significantly less often than expected by chance ($\chi^2 = 11.75$, d.f. = 4, P < 0.02). The most common initial response of the ant to the bite was to groom the affected appendage (18/26 trials). In 2/26 trials the initial response was to autotomize or attempt to autotomize the bitten appendage; in 2/26 trails the initial response was body spasm; in 1/26 trails the ant shook the bitten leg; in 1/26 trials the initial response was rapid paralysis; and in 2/26 trials the initial response was not recorded (the time between bite and paralysis was too rapid).

Subsequent reactions to the bite included selfamputation, or autotomy, of the bitten limb, body spasms, abdominal contractions resulting in a twisting of the abdomen to the side, and, eventually, paralysis. In 4/26 trials, the ant autotomized the bitten limb between approximately 10 sec and 3.67 min from being bitten (mean \pm s.d.: 1.25 \pm 1.63 min). In 12/26 of the trials, spiders bit the ants multiple times. In all but one trial, the attack by *Z*. *rubidum* resulted in complete paralysis of the ant. In that one trial, the ant autotomized the bitten leg within 15 sec of being bitten. After 17 min the ant was still active and apparently unaffected and the trial was ended.

The average time to complete paralysis was 7.85 min (s.d. = 4.72 min, n = 25). We decided to determine if the time to paralysis was influenced by the size of the spider as, presumably, larger spiders might deliver more venom. Therefore, we compared the mean time to paralysis for the three different Size Classes. The mean time to paralysis for Size Class A spiders was $8.35 \pm 2.67 \min(n = 4)$; the mean time to paralysis for Size Class B spiders was $6.77 \pm 4.38 \text{ min } (n = 10)$; and the mean time for Size Class C spiders was $8.67 \pm 5.63 \min(n =$ 11). We used the GT2 method for multiple comparisons of means for unequal sample sizes (Sokal & Rohlf 1981) and found no statistical difference in the time between initial bite and complete paralysis of the ant for the three Size Classes of spiders $(m_{.05[3,22]} = 2.584, P > 0.05$ for all pairwise comparisons).

Ants were bitten multiple times in all trials (4/4)with Size Class A spiders, in 2/9 trials with Size Class B spiders, and in 5/11 trials with Size Class C spiders. Ants autotomized the bitten appendage in two trials with Size Class B spiders and in one trial with a Size Class C spider (the fourth instance of autotomization resulted in no paralysis of the ant and was not included in the analysis). Since multiple bites and autotomization of the bitten limb may affect the time to paralysis, we eliminated these trials from the data set to determine if there was a difference in time to paralysis between the different spider Size Classes. In this comparison, the mean time to paralysis for Size Class B spiders was $5.33 \pm 3.97 \min (n = 6)$ and the mean time to paralysis for Size Class C spiders was 7.10 ± 7.60 min (n = 5) resulting in no significant difference in the time to paralysis $(m_{.05[1,9]} = 2.262, P > 0.05)$. It is important to note that the size of the ants fed to the spiders was not measured. However, all ants were 4 mm or less in length and, subjectively, appeared to be approximately similar in size.

From our observations of live Z. rubidum, it appears that spiders usually remained inside their retreats during the day, emerging to hunt ants at night. Upon encountering an ant, Z. rubidum typically bit a rear leg rather than a front appendage or the body of the ant. The ant usually reacted immediately to the bite by grooming the bitten appendage. In some instances, the ant autotomized the bitten appendage and, in one such instance, this autotomization of the leg apparently prevented the venom from paralyzing the ant. Often the spider re-approached the ant to deliver one or more additional bites. In all but the one instance mentioned above, the end result of these bites was complete paralysis of the ant.

Once the ant stopped moving, the spider approached and touched the ant with its first pair of legs. If the ant did not respond, the spider carried the ant to a secluded place (under a rock or near its retreat) using its fangs and palpal claws to carry the ant and began feeding on the ant. Couvreur (1990b) also reported the tendency of *Z. rubidum* to carry the ant to a secluded place for consumption. Couvreur (1990a) proposed that the spider used this paralyzed ant as a type of disguise and protection against attacks by other members of the ant colony when the spider foraged near the colony entrance.

Spiders of the family Zodariidae possess a series of one to 15 modified setae on the dorsolateral surface of the femora. These flattened setae have openings to secretory pores at the bases, and the hairs + pores are collectively referred to as the femoral organ (Jocqué 1988, 1991). Jocqué and Billen (1987) suggest that the femoral organ found on zodariids, particularly in the genus Zodarion, may be involved in prey capture. They suggest that the secretions produced by the femoral organ may act to subdue the ant. Santschi (1908) and Harkness (1976) indicate that an ant appeared to be subdued when a spider apparently touched the ant with the front legs and did not necessarily require a bite. However, our observations do not support the role of the femoral organ suggested by Jocqué and Billen (1987). In our experiments, paralysis of the ants ensued only after the spider bit one or more of the appendages (legs or antennae). Contact by the spider's front legs, as occurred on several instances when a spider first approached a passing ant, was not sufficient to subdue the ants. Jocqué (1988) and Couvreur (1990b) also indicate that a bite from the spider is necessary to subdue the ant. The attack by the spider, as pointed out by Harkness (1976), is often extremely rapid so that administration of a bite by the spider may not be clearly discernable unless the attack itself is observed with the aid of a microscope.

A variety of spiders engage in myrmecophagy. Ants are abundant in most terrestrial ecosystems but, due to their defensive capabilities (Hölldobler & Wilson 1990), specialized capture techniques have evolved among many myrmecophages. Larger more robust myrmecophagic spiders, such as different species of jumping spiders (Salticidae), have been observed to position themselves facing their ant prey, attacking head-on (Edwards et al. 1975; Cutler 1980; Li et al. 1999). This frontal attack allows the spider to grasp the prey by the alitrunk making it difficult or impossible for the ant to defend itself. Spiders in the family Theridiidae rely on silk to capture ants, often building their webs in close proximity to ant nests (Hölldobler 1970, Porter & Eastmond 1981; MacKay 1982; Clark 1996). Euryopis coki Levi 1954 was observed securing a worker of *Pogonomyrmex* with a strand of silk then biting it on the leg while the ant was tethered to the ground (Porter & Eastmond 1981). In contrast, the small size of Zodarion spiders makes frontal attacks impractical and risky and silk is not used by these spiders to immobilize the prey. Spiders of the genus Zodarion (Zodariidae) have, instead, adopted a hit and run approach to hunting ants, composed of an attack to the rear appendages and a short withdrawal until the ant becomes paralyzed (Schneider 1971; Harkness 1976, 1977; Couvreur 1990b; present study).

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